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# Ten-year height growth of open-pollinated black spruce families in Ontario

T.J.B. Boyle

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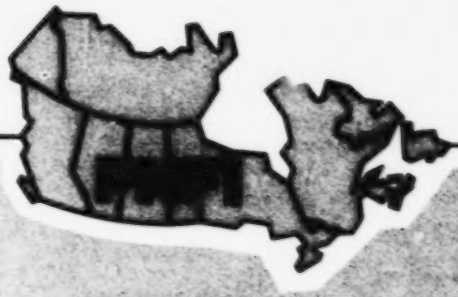
Petawawa National Forestry Institute



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# TEN-YEAR HEIGHT GROWTH OF OPEN-POLLINATED BLACK SPRUCE FAMILIES IN ONTARIO

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**Cover:** Black spruce seedlings

## ABSTRACT

Results of 10-year height growth in three series of open-pollinated progeny tests of black spruce (Picea mariana (Mill.) B.S.P.), in three site regions of northern Ontario, are presented. Estimates of narrow sense heritability from individual test sites ranged from 0 to 0.399 for single trees and from 0 to 0.896 for families, with averages of 0.169 and 0.663 respectively. Estimates from multi-location analyses ranged from 0.099 to 0.152, with an average of 0.124 for single trees, and from 0.836 to 0.930, with an average of 0.884 for families. The family x environment interaction was significant in all three series.

By means of an overlapping cluster analysis method, four or five genetic breeding zones were delineated for each site region. Proposals are made for breeding zones which, as far as possible, take account of both genetic breeding zones and administrative boundaries.



## RÉSUMÉ

Ce rapport présente les résultats de la croissance décennale en hauteur de trois séries de tests de descendance de l'épinette noire (Picea mariana [Mill.] B.S.P.), obtenue par pollinisation libre, dans trois régions du nord de l'Ontario. Dans chaque plantation expérimentale, l'héritabilité estimative au sens strict variait de 0 à 0,399 dans le cas des arbres pris individuellement et de 0 à 0,896 dans le cas des familles, la moyenne étant respectivement de 0,169 et 0,663. Dans l'ensemble des plantations, elle variait de 0,099 à 0,152 dans le cas des arbres pris individuellement et de 0,836 à 0,930 dans celui des familles, la moyenne étant respectivement de 0,124 et 0,884. Dans les trois séries, l'interaction famille-milieu était significative.

Par l'analyse de grappes se recouvrant partiellement, on a délimité dans chaque région quatre ou cinq zones d'amélioration génétique. Des zones d'amélioration sont proposées. Dans la mesure du possible, elles s'inspirent à la fois des zones d'amélioration génétique et des limites administratives.

# TEN-YEAR HEIGHT GROWTH OF OPEN-POLLINATED BLACK SPRUCE FAMILIES IN ONTARIO

## INTRODUCTION

Progress in tree improvement depends on the adoption of optimally-designed breeding strategies. The design of a suitable strategy is, in turn, determined by the genetic and silvical characteristics of the species. Black spruce (Picea mariana (Mill.) B.S.P.) typically exhibits little variation in crown or stem form and, consequently, the major character on which selection should be based is growth rate (Morgenstern 1975). In many species, narrow sense heritability of volume or height growth has been found to be relatively low (Zobel and Talbert 1984). The same situation has been demonstrated for nursery-grown black spruce (Morgenstern 1973). In addition, black spruce produces seed regularly and prolifically from around the age of six years (Heinselman 1957). These factors have resulted in the development of genetic improvement strategies for black spruce based on the establishment of seedling seed orchards and associated open-pollinated progeny tests (Coles 1979, Rauter 1980).

Beginning in 1970, three series of open-pollinated progeny tests were established by the Petawawa National Forestry Institute covering the three ecological regions of Ontario (Hills 1961) where black spruce is a major commercial species. The objectives of these tests were:

(a) to obtain genetic parameters to assist in the planning of breeding programs, and
(b) to identify superior families for inclusion in seed orchards (Morgenstern 1978).

The estimation of heritability from open-pollinated progeny tests requires certain assumptions, which include:

1. Regular, diploid, Mendelian inheritance
2. Linkage equilibrium
3. Progeny are not inbred
4. Progeny are random members of a non-inbred population
5. Progeny belonging to the same family are half-sibs
6. No epistasis
7. No maternal effects (Stonecypher 1966).

Several of these assumptions, particularly numbers 3, 4, and 5 are likely to be at least partially invalid, leading to possible overestimates of heritability (Namkoong 1966, Squillace 1974). Although controlled pollination tests may be expected to give more reliable estimates of heritability, the ease and speed with which open-pollinated tests can be established allow rapid estimates to be obtained from large samples of material (Morgenstern 1975). This factor is of particular relevance for black spruce, given the scarcity of published estimates of heritability, especially from older material. From a variety of open- and controlled-pollination progeny tests, single tree, narrow sense heritabilities that range from 0.18 to 0.42 have been estimated for

height growth in black spruce (Morgenstern 1973, 1974, 1975, Giberson 1983). However, the oldest trees measured were only five years from seed.

Hills (1961) delineated "site regions" in Ontario, based on ecological data, which are quite extensive - region 3E amounts to 115 000 km² (Map 1). Due to variation in the relative response of populations and families within populations to different environments, it is likely that each site region should be divided into a number of separate or overlapping breeding zones, within which different parents are used for the establishment of breeding and seed production populations. Results from multiple-location progeny tests can be useful in helping to delineate these breeding zones. Currently, in Ontario, each administrative region is responsible for the design and implementation of its own tree improvement programme, resulting in very different strategies being adopted by neighbouring regions (J.V. Hood, pers. comm.). Some genetic guidelines for the delineation of breeding zones are, therefore, vitally important if genetic gains are to be optimized.

## MATERIALS AND METHODS

In each of the three site regions, seven to nine populations were sampled, with between four and 36 single-tree, open-pollinated seed collections being made in each population (Table 1, Map 1). All three series of tests were planted in a randomized complete block design, with three replications of nine-tree (3x3) square plots, using four-year-old nursery stock.

Seven tests, designated as the "G-series" were established in site region 3E (Hills 1961) in autumn 1974 and spring 1975 (Morgenstern 1978). One test was established in each of the six site districts of Region 3E, with a second test in the large Cochrane district (Morgenstern 1972). A total of 132 families was included in the G series, with between 90 and 124 families represented in individual tests (Table 2, Map 1).

The "I series" of six tests were established in site region 3W in spring 1976. A total of 115 families was used, with each test containing between 70 and 87 families (Table 2). Test I8 (Crystal River) was burnt in 1976 but replaced in the following year with surplus stock.

Six tests, constituting the "J series", were established in spring 1977 in site region 4S. Each test contained between 57 and 74 families from a total of 102 families used.

Heights were recorded in all tests when the trees were 10 years old from seed, between 1980 and 1982. An analysis of variance by individual test sites was carried out on the measurements, according to the following models:

(a) Individual tree:

$$y_{ijkl} = \mu + P_{ijk} + e_{ijkl}$$

where $y_{ijkl}$ = height of the lth tree in the kth family from the jth stand, planted in the ith replication.

**Table 1. Populations sampled**

G. Series: Site Region 3E

| Pop. No. | Location | Long. (°W) | Lat. (°N) | No. of families |
|---|---|---|---|---|
| 50 | Timagami | 79°55' | 47°05' | 4 |
| 51 | Lake Abitibi | 80°10' | 48°50' | 8 |
| 6906 | Foleyet | 82°23' | 48°12' | 15 |
| 6907 | Timmins | 81°25' | 48°32' | 15 |
| 6908 | Iroquois Falls | 80°38' | 48°59' | 15 |
| 6909 | Otasawin River | 85°05' | 49°45' | 15 |
| 6914 | White River | 85°20' | 48°38' | 13 |
| 6915 | Manitouwadge | 85°47' | 49°08' | 11 |
| 73 | Moonbeam Seed Orchard | 82°30' | 49°20' | 36 |

I Series: Site Region 3W

| Pop. No. | Location | Long. (°W) | Lat. (°N) | No. of families |
|---|---|---|---|---|
| 93 | Woodlands Nursery | 86°20' | 49°45' | 11 |
| 6910 | Beardmore | 87°50' | 49°40' | 14 |
| 6916 | Armstrong | 89°11' | 50°18' | 15 |
| 6917 | Upsala | 90°27' | 49°00' | 15 |
| 6918 | Ignace | 91°31' | 49°25' | 15 |
| 6919 | Savant Lake | 90°41' | 50°19' | 16 |
| 6920 | Minchin Lake | 90°34' | 50°44' | 15 |
| 6932 | Shebandowan | 90°11' | 48°40' | 14 |

J. Series: Site Region 4S

| Pop. No. | Location | Long. (°W) | Lat. (°N) | No. of families |
|---|---|---|---|---|
| 6918 | Ignace | 91°31' | 49°25' | 13 |
| 6922 | Sioux Lookout | 91°40' | 50°13' | 15 |
| 6923 | Perrault Falls | 93°20' | 50°24' | 14 |
| 6924 | Red Lake | 93°44' | 50°53' | 14 |
| 6925 | Vermillion Bay | 93°30' | 49°50' | 17 |
| 6928 | Atikokan | 91°40' | 48°44' | 14 |
| 6931 | Nestor Falls | 93°55' | 49°20' | 15 |

Map 1. Location of test sites and parent stands for the three series of open-pollinated progeny tests in Northern Ontario

Site region 3E 353-G Series
Site region 3W 353-I Series
Site region 4S 353-J Series

■ location of test sites

▲ Stands in regions

Note: Families from stand 7300 were used in both the G and I series; and families from stand 6918 were used in both the I and J series.

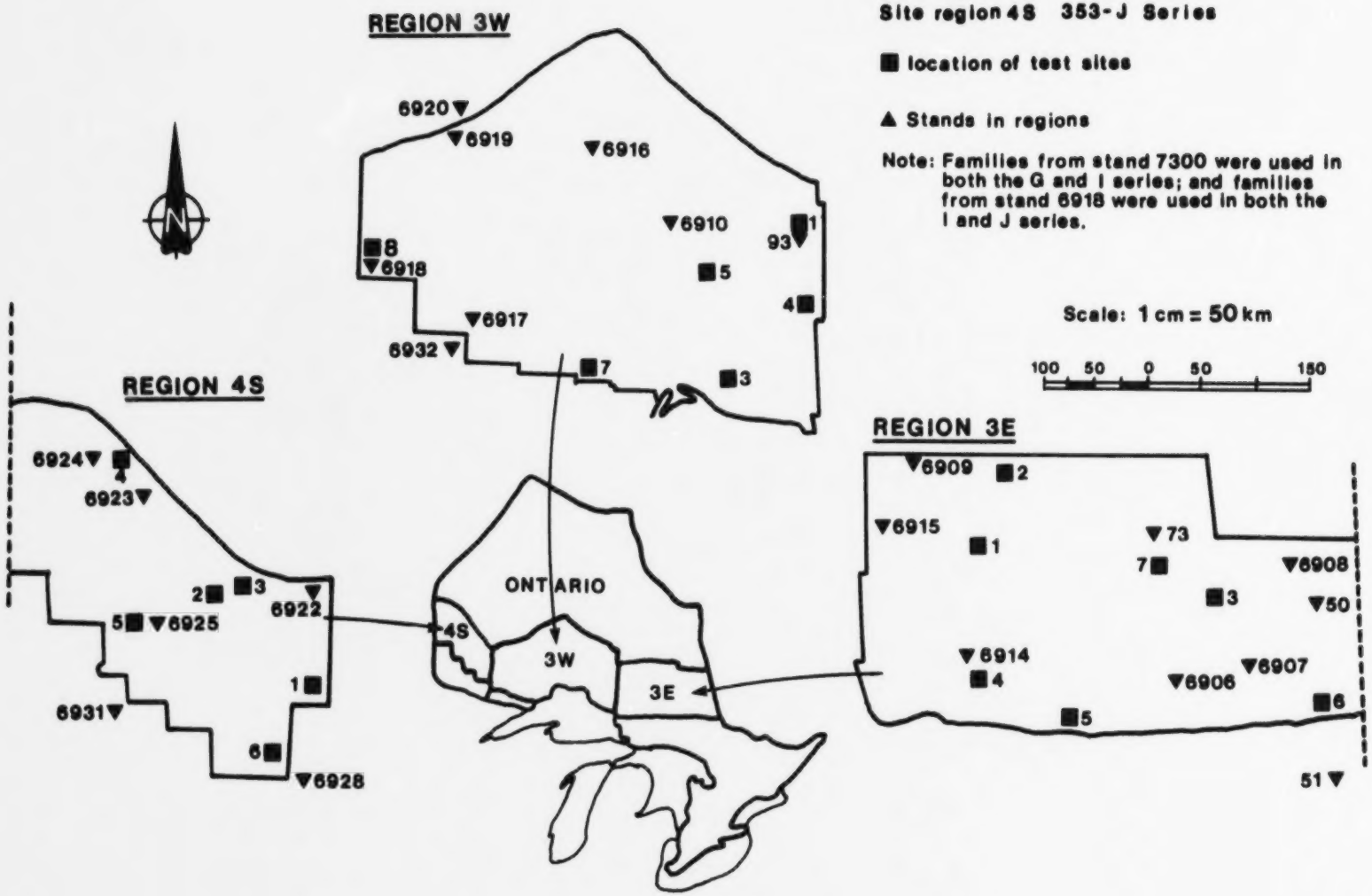


**Table 2. Test locations**

G. Series: Site Region 3E

| Test | Location | Long. (°W) | Lat. (°N) | No. of stands | No. of families |
|---|---|---|---|---|---|
| G1 | Hornepayne, Farquhar Twp. | 84°30' | 49°2`' | 9 | 124 |
| G2 | Hearst, Rogers Twp. | 84°10' | 49°55' | 7 | 90 |
| G3 | Cochrane, Duff Twp. | 81°06' | 48°50' | 7 | 92 |
| G4 | White River, Dahl Twp. | 85°00' | 48°20' | 9 | 106 |
| G5 | Chapleau, Marshall Twp. | 83°22' | 47°57' | 9 | 99 |
| G6 | Kirkland Lake, Dunmore Twp. | 80°21' | 48°10' | 9 | 110 |
| G7 | Kapuskasing, Nansen Twp. | 82°07' | 49°28' | 7 | 101 |

I Series: Site Region 3W

| Test | Location | Long. (°W) | Lat. (°N) | No. of stands | No. of families |
|---|---|---|---|---|---|
| I1 | Geraldton, Hoiles Creek | 86°25' | 49°40' | 8 | 78 |
| I3 | Geraldton, Aguasabon River | 87°10' | 48°55' | 8 | 70 |
| I4 | Manitouwadge | 86°05' | 49°10' | 8 | 76 |
| I5 | Nipigon, Sturgeon River | 87°15' | 49°35' | 8 | 87 |
| I7 | Thunder Bay, Camp 11 | 89°07' | 48°40' | 8 | 84 |
| I8 | Ignace, Crystal River | 91°25' | 49°45' | 8 | 80 |

J Series: Site Region 4S

| Test | Location | Long. (°W) | Lat. (°N) | No. of stands | No. of families |
|---|---|---|---|---|---|
| J1 | Ignace, Milky Lake | 91°55' | 50°45' | 7 | 57 |
| J2 | Dryden, Rugby Twp. | 93°00' | 49°55' | 7 | 57 |
| J3 | Sioux Lookout, Lomond Twp. | 92°25' | 50°05' | 7 | 74 |
| J4 | Red Lake, Dixie Creek | 93°45' | 50°50' | 7 | 73 |
| J5 | Kenora, Sheila Lake | 93°52' | 49°40' | 7 | 69 |
| J6 | Fort Francois, Mines Centre | 92°25' | 48°40' | 7 | 62 |

$\mu$ = experimental mean height,

$P_{ijk}$ = effect of ijkth plot, and

$e_{ijkl}$ = within-plot error

(b) Plot means:

$$y_{ijk} = \mu + r_i + s_j + f_{(kj)} + e_{ijk}$$

where $y_{ijk}$ = mean of kth family from jth stand in ith replication.

$\mu$ = experimental average of plot means,

$r_i$ = effect of ith replication,

$s_j$ = effect of jth stand,

$f_{(kj)}$ = effect of kth family from jth stand, and

$e_{ijk}$ = residual between-plot error (family x replication)

These two models result in analysis of variance tables and expected mean squares as shown in Table 3, yielding estimates of narrow sense heritability according to the following formulae:

(a) Single tree $h^2 = \dfrac{4\,\sigma_f^2}{\sigma_w^2 + \sigma_p^2 + \sigma_s^2 + \sigma_f^2}$

where $\sigma_f^2$ = variance component due to families within stands,

$\sigma_s^2$ = variance component due to stands,

$\sigma_p^2$ = variance component due to residual between-plot error,

$\sigma_w^2$ = variance component due to within-plot error.

(b) Family $h^2 = \dfrac{\sigma_f^2}{\frac{\sigma_w^2}{nrs} + \frac{\sigma_p^2}{rs} + \frac{\sigma_s^2}{s} + \sigma_f^2}$

where n = harmonic mean number of trees per plot,

r = number of replications,

**Table 3. Analysis of variance tables**

1. Individual locations, within plot analysis.

| Source | df | EMS |
|---|---|---|
| Among plots | rsf-1 | |
| Within-plot error | rsf(n-1) | $\sigma^2_w$ |

2. Individual locations, among-plot means analysis.

| Source | df | EMS |
|---|---|---|
| Replications | r-1 | |
| Stands | s-1 | $\sigma^2_w/n + \sigma^2_p + r\sigma^2_f + rf\sigma^2_s$ |
| Families within stands | s(f-1) | $\sigma^2_w/n + \sigma^2_p + r\sigma^2_f$ |
| Residual error among plots | (sf-1)(r-1) | $\sigma^2_w/n + \sigma^2_p$ |

3. Over all locations, among-plot means analysis.

| Source | df | EMS |
|---|---|---|
| Locations | t-1 | |
| Replications within locs | t(r-1) | |
| Stands | s-1 | $\sigma^2_w/n + \sigma^2_p + t\sigma^2_g + tr\sigma^2_f + trf\sigma^2_s$ |
| Families within stands | s(f-1) | $\sigma^2_w/n + \sigma^2_p + t\sigma^2_g + tr\sigma^2_f$ |
| Gen x env interaction | (t-1)(sf-1) | $\sigma^2_w/n + \sigma^2_p + t\sigma^2_g$ |
| Residual error among plots, within locs | t(r-1)(sf-1) | $\sigma^2_w/n + \sigma^2_p$ |

where f = average number of families per stand, and all other symbols are explained in the text.

s = number of stands.

A coefficient of 4, the theoretically expected value for half-sibs, was used in the formula for single tree heritability. The weaknesses in the assumptions noted above and the small effective male populations found in some species (eg. Cheliak 1983) should reduce this coefficient. However, effective population sizes for several populations of black spruce in New Brunswick were found to be quite large (Boyle 1985a) and, in the absence of any other information, the theoretically expected coefficient should be satisfactory. F eachor series of tests, an analysis of variance over all locations was also undertaken. The model for the within-plot analysis was identical to that for individual locations, other than an additional subscript due to locations, but for the analysis of plot means the following model was used:

$$y_{ijkl} = \mu + t_l + r_{(il)} + s_j + f_{(kj)} + g_{jkl} + e_{ijkl}$$

where $y_{ijkl}$ = mean of kth family from jth stand in ith replication, planted at the lth test site,

$t_l$ = effect of lth test site,

$\mu$ = average of plot means over all test sites,

$r_{(il)}$ = effect of ith replication in the lth test site,

$g_{jkl}$ = family x environment interaction between the jkth family and the lth location,

$e_{ijkl}$ = residual between-plot, within-site error, and

$s_j$ and $f_{(kj)}$ are as previously defined.

This model yields an analysis of variance table and expected mean squares as shown in Table 3, resulting in estimates of narrow sense heritability according to the following formulae:

$$\text{(a) Single tree } h^2 = \frac{4\,\sigma^2_{f'}}{\sigma^2_{w'} + \sigma^2_{p'} + \sigma^2_{g'} + \sigma^2_{s'} + \sigma^2_{f'}}$$

$$\text{(b) Family } h^2 = \frac{\sigma^2_{f'}}{\frac{\sigma^2_{w'}}{ntrs} + \frac{\sigma^2_{p'}}{trs} + \frac{\sigma^2_{g}}{ts} + \frac{\sigma^2_{s'}}{s} + \sigma^2_{p'}}$$

where $\sigma^2_g$ = variance component due to the genotype x environment interaction,

t = the number of test sites, and primes are used to distinguish multilocation from single location estimates of components of variance.

Burdon (1977) suggested that in forest tree breeding, in contrast to crop breeding, greater emphasis should be placed on the influence of environments, rather than of the genotypes in genotype x environment interactions. This is because of the longer time scale during which trees are influenced by an environment, over which little control can be exercised, compared with annual crop plants. Since new genotypes are constantly being produced for use on relatively constant environments, progeny test results should be used for characterizing the environments.

Environments which produce similar results in progeny tests would presumably behave similarly under commercial plantation conditions and should, therefore, belong to the same breeding zone. For delineating breeding zones, two environments having different productivities, but which rank families identically, are more similar than two environments having the same productivity, but which produce different rankings (Fox and Rosielle 1982).

Burdon (1977) suggested that genetic correlations among test locations are useful in studying the role of environments, because some of the statistical deficiencies of the analysis of variance are avoided. Genetic correlations ($r_{gxy}$) are given by:

where $r_{gxy} = r_{xy} / (h_x \cdot h_y)$

$r_{xy}$ = correlation among group mean ranks at locations x and y;

and

$h^2_x$ and $h^2_y$ are the heritabilities of group means at locations x and y

Therefore, for each test series, the environments were grouped together by cluster analysis based on genetic correlations among rankings (SAS Institute Inc. 1982: Procedure VARCLUS). To take account of the different families and different numbers of families at each test site, the ranks were expressed as proportions. Thus, the family which ranked 62nd out of the 124 families at site G1 would have an identical rank (0.5) to that family which ranked 45th out of the 90 families at site G2.

One weakness of rigid breeding zones is that dividing lines must separate the zones. This means that no matter where the lines are drawn, sites which are adjacent, and quite similar to each other, may be placed in separate breeding zones. One way to overcome this problem is to devise overlapping breeding zones. These are genetically more satisfactory, but administratively a greater, but not insurmountable, problem.

Therefore, a method of cluster analysis producing overlapping clusters (Sarle 1983: Procedure OVERCLUS) was applied to the genetic correlations, based on rankings, calculated for each pair of sites.

As the correlations are based on ranks, rather than raw data, the family heritabilities should also be based on ranks. In order to make an estimate of family heritability of ranks, the ranking of a family in each of the three replications at a site was treated as an individual observation of the

character. Therefore, an analysis of variance could be carried out according to the following model:

$$y_{ijk} = \mu + s_i + f_{(ij)} + e_{ijk}$$

where $y_{ijk}$ = rank of the jth family from the ith stand in the kth replication

$s_i$ = effect of ith stand

$f_{(ij)}$ = effect of jth family

$e_{ijk}$ = residual error.

"Family rank heritability" was then given as:

$$\text{Family rank } h^2 = \frac{\sigma_f^2}{\frac{\sigma_e^2}{rs} + \frac{\sigma_s^2}{s} + \sigma_f^2}$$

where $\sigma_e^2$ is the component of variance due to residual error, and all other symbols are as previously defined. In practice, however, the genetic correlations calculated using "family rank heritability" and regular family heritability in the denominator were very similar and produced virtually identical results from the cluster analyses.

From the cluster analyses, homogeneous "genetic breeding zones" were identified. The families and stands represented at the test sites with each breeding zone were ranked by their average performance in that zone. Groups of families among which performance did not differ significantly were identified using the means separation method of Scott and Knott (1974) using an adaptation of the FORTRAN program prepared by Gates and Bilbro (1978).

## RESULTS AND DISCUSSION

1. Heritability and variance components.

Estimates of components of variance and narrow sense heritabilities on a single tree and a family basis, by individual location, are given in Table 4. Heritability estimates ranged from 0 to 0.399 for individual trees and from 0 to 0.896 for families. The zero estimates were obtained from test site G1, where a negative variance component was estimated for families within stands. The averages over all test sites were 0.169 for single tree heritability and 0.663 for family heritability.

At all test sites, the within-plot component of variance was easily the largest, followed by the among-plot residual error. In most cases, the component of variance due to families within stands was larger than that for stands. This was particularly true for the J-series, where the former was, on average, more than 10 times the size of the latter. However, in the G-series, the family component of variance, averaged only about 50 per cent larger than the stand component of variance, whilst in the I-series, the difference was even smaller.

**Table 4. Estimates of components of variance and narrow sense heritabilities for each test site and for each series of tests**

G Series

| | G1 | G2 | G3 | G4 | G5 | G6 | G7 | Mean | Multi |
|---|---|---|---|---|---|---|---|---|---|
| $\sigma^2_w$ = | 532.84 | 681.20 | 686.55 | 288.83 | 486.24 | 444.93 | 215.11 | | 477.09 |
| $\sigma^2_p$ = | 273.18 | 256.25 | 138.93 | 125.84 | 88.37 | 260.50 | 102.24 | | 234.43 |
| $\sigma^2_g$ = | | | | | | | | | 17.52 |
| $\sigma^2_f$ = | -12.81 | 38.40 | 26.23 | 13.13 | 66.15 | 10.73 | 14.54 | | 18.66 |
| $\sigma^2_s$ = | 9.93 | 25.42 | 13.44 | 11.20 | 22.74 | 15.40 | 12.14 | | 7.89 |
| $h^2_s$ = | 0.000 | 0.153 | 0.121 | 0.120 | 0.399 | 0.059 | 0.169 | 0.146 | 0.099 |
| $h^2_f$ = | 0.000 | 0.648 | 0.641 | 0.630 | 0.880 | 0.438 | 0.626 | 0.552 | 0.886 |

I Series

| | I1 | I3 | I4 | I5 | I7 | I8 | Mean | Multi |
|---|---|---|---|---|---|---|---|---|
| $\sigma^2_w$ = | 602.28 | 596.90 | 792.33 | 556.94 | 899.48 | 363.08 | | 628.06 |
| $\sigma^2_p$ = | 192.03 | 70.14 | 185.37 | 106.62 | 233.12 | 210.79 | | 140.96 |
| $\sigma^2_g$ = | | | | | | | | 16.36 |
| $\sigma^2_f$ = | 30.48 | 64.26 | 37.58 | 50.54 | 21.41 | 6.20 | | 25.20 |
| $\sigma^2_s$ = | 15.55 | 24.09 | 92.01 | 32.28 | 18.18 | 9.28 | | 24.06 |
| $h^2_s$ = | 0.145 | 0.340 | 0.136 | 0.271 | 0.073 | 0.042 | 0.175 | 0.121 |
| $h^2_f$ = | 0.727 | 0.896 | 0.662 | 0.842 | 0.605 | 0.395 | 0.697 | 0.836 |

J Series

| | J1 | J2 | J3 | J4 | J5 | J6 | Mean | Multi |
|---|---|---|---|---|---|---|---|---|
| $\sigma^2_w$ = | 856.78 | 855.79 | 705.09 | 1087.81 | 565.69 | 918.56 | | 828.90 |
| $\sigma^2_p$ = | 259.88 | 341.12 | 391.44 | 318.47 | 143.18 | 103.73 | | 233.13 |
| $\sigma^2_g$ = | | | | | | | | 20.17 |
| $\sigma^2_f$ = | 46.92 | 58.76 | 49.16 | 73.28 | 42.98 | 61.98 | | 42.61 |
| $\sigma^2_s$ = | 5.98 | 3.41 | -8.43 | 11.00 | 2.09 | -3.71 | | -1.85 |
| $h^2_s$ = | 0.160 | 0.187 | 0.172 | 0.197 | 0.228 | 0.229 | 0.189 | 0.152 |
| $h^2_f$ = | 0.714 | 0.728 | 0.682 | 0.777 | 0.797 | 0.848 | 0.758 | 0.930 |

Note: $\sigma^2_w$ = within-plot error variance component

$\sigma^2_p$ = residual between-plot error variance component

$\sigma^2_g$ = genotype x environment variance component

$\sigma^2_f$ = family within-stand variance component

$\sigma^2_s$ = stand variance component

$h^2_s$ = narrow sense heritability based on individual trees

$h^2_f$ = narrow sense heritability based on family means

"Multi" = estimates from analysis over all tests within a series

Estimates from the multi-location analyses are also given in Table 4. The results tend to agree quite closely with those from individual locations. For example, the G-series produced the smallest estimate for single tree heritability (0.099) and the J-series produced the largest estimates, both for single tree (0.152) and family heritability (0.930). Also, the component of variance due to stands, in proportion to the component due to families within stands, was largest in the I-series and smallest in the J-series where, in fact, a negative estimate was obtained.

The estimates of heritability given above are, of course, based on quite young (10-year-old) material. The use of heritabilities estimated from young material in estimating future genetic gains is suspect for several reasons. Firstly, such estimates are usually based on individual growth rate free from tree-to-tree competition. In closed canopy conditions, families or individuals selected for fast early growth may not maintain their superiority, and accelerated stand development may lead to increased mortality (Cannell 1982, Talbert 1982). Also, it has been shown for several species that estimates of heritability for height growth tend to decrease with age (Namkoong et al. 1972, Ying and Morgenstern 1979, Birot and Christophe 1983). Although estimates from 10-year-old material will still suffer from some of these problems, they will be far more reliable than estimates from nursery tests, which have provided the bulk of heritability estimates in black spruce to date.

Certainly, with an average multi-location estimate of 0.124 for single-tree heritability, compared with Morgenstern's (1973, 1974, 1975) estimates ranging from 0.18 to 0.42 for nursery age material, there seems to be a decrease with age for black spruce. Birot and Christophe (1983) found that for both Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) and Sitka spruce (Picea sitchensis (Bong.) Carr.), estimates of heritability tended to stabilize after about six years of age, so the estimates obtained from this study may fairly well reflect future estimates from older material.

The very great differences, in all cases, between estimates of single-tree and family heritabilities emphasize the effectiveness of progeny testing in selecting superior genotypes, in comparison with phenotypic mass selection. These results suggest that, for black spruce, a rapid and inexpensive approach to plus tree selection, followed by progeny testing, will produce much larger genetic and economic gains than an intensive, time-consuming, plus tree selection programme without progeny testing.

Differences among sites, replications within sites, and families within stands were significant at the 0.1 per cent level in all three series. Differences among stands were significant at the 0.1 per cent level in the G- and I-series, but were nonsignificant in the J-series. The genotype-environment interaction was significant at the 1 per cent level in the G- and I-series, but only at the 5 per cent level in the J-series.

The apparent differences in proportions of family and stand variance components in the three series of tests may be due to random error, to differences in sampling procedure, or to real differences in population structure in the three site regions. Almost all of the stands used in these tests were included in a series of range-wide provenance tests planted in five locations across Ontario. At 15 years from seed in those tests, the G-series

stands ranked between 23rd and 62nd out of a total of 76 provenances; those in the I-series ranked between 5th and 30th, whilst those in the J-series were between 4th and 42nd (Boyle 1985b). In terms of variation in performance among the stands therefore, it does not appear as though the I-series should be more variable than the others. An examination of the population structure within and among the stands in each series, by means of isozyme analysis, is necessary to further investigate these differences.

2. Genetic correlations.

Matrices of genetic correlations based on family mean ranks, among test sites for each series, are given in Table 5. Genetic correlations with site 1 in the G-series could not be calculated due to the zero estimate of family heritability. Apart from correlations between a location and itself, genetic correlations ranged from -0.257 between sites J3 and J4 to 0.762 between sites I5 and I7. In general, genetic correlations among adjacent sites tended to be larger than those between geographically distant sites.

3. Breeding zones.

The significant genotype x environment interactions found for all three series indicate that the site regions should not be considered as single breeding zones. For each series, two discrete clusters could be separated based on genetic correlations of family ranks (Table 6). In both the I-series and the J-series, these clusters were geographically distinct. I7 and I8 were clustered separately from the other I locations, and J1, J2, and J3 formed a separate, distinct group. In the G-series, geographically distant locations were clustered together, while neighbouring sites were, in some cases, separated.

With overlapping cluster analysis, any number of clusters, up to a maximum of $2^n - 1$ clusters for n locations, can be identified. However, for greater numbers of clusters, the computer resources required increase rapidly (Sarle 1983). In any case, with only six or seven locations, the number of meaningful clusters is limited. Therefore, a maximum of three clusters was specified for each series, and the results are given in Table 6. In contrast to the discrete clusters, in every case except one, the overlapping clusters formed were geographically distinct. The one exception was in the J-series where the third cluster included locations 1, 2, and 4, but not 3.

As mentioned earlier, overlapping breeding zones would be administratively difficult to handle. However, overlapping clusters can be combined to give non-overlapping breeding zones. For example, in the J-series, site 2 occurs in all three clusters and, when all these clusters are considered, it is associated with every other site (Table 6). On the other hand, site 3 occurs only in clusters 1 and 2, where it is associated with sites 1, 2, 5, and 6, but not with site 4. Therefore, site 2 should be placed in a separate breeding zone from site 3. Results from all sites should be considered in selecting superior genotypes for the site 2 breeding zone, but only results from sites 1, 2, 3, 5, and 6 should be used for the site 3 breeding zone. Sites 5 and 6 occur together in a third breeding zone, for which results from sites 2, 3, 5, and 6 should be used, and site 4 forms the fourth breeding zone, within which genotypes should be selected based on results at sites 1, 2, and 4. Site 1 would constitute a fifth breeding zone, but is actually

Table 5. Genetic correlations for 10-year ranks among all test sites in each series

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| G-series | | | | | | | |
| Site 1 | - | | | | | | |
| Site 2 | - | 1.543 | | | | | |
| Site 3 | - | 0.175 | 1.560 | | | | |
| Site 4 | - | -0.022 | -0.116 | 1.587 | | | |
| Site 5 | - | 0.123 | -0.097 | 0.499 | 1.136 | | |
| Site 6 | - | 0.319 | 0.470 | 0.314 | 0.422 | 2.283 | |
| Site 7 | - | 0.165 | 0.412 | -0.150 | -0.168 | 0.317 | 1.597 |
| | Site 1 | Site 2 | Site 3 | Site 4 | Site 5 | Site 6 | Site 7 |
| I-series | | | | | | | |
| Site 1 | 1.292 | | | | | | |
| Site 3 | 0.241 | 1.131 | | | | | |
| Site 4 | 0.703 | 0.681 | 1.460 | | | | |
| Site 5 | 0.328 | 0.560 | 0.574 | 1.176 | | | |
| Site 7 | 0.065 | 0.324 | 0.551 | 0.762 | 1.767 | | |
| Site 8 | 0.446 | -0.011 | 0.143 | 0.306 | 0.596 | 2.353 | |
| | Site 1 | Site 3 | Site 4 | Site 5 | Site 7 | Site 8 | |
| J-series | | | | | | | |
| Site 1 | 1.401 | | | | | | |
| Site 2 | 0.440 | 1.374 | | | | | |
| Site 3 | 0.311 | 0.600 | 1.466 | | | | |
| Site 4 | 0.341 | 0.280 | -0.257 | 1.285 | | | |
| Site 5 | 0.074 | 0.161 | 0.350 | 0.093 | 1.255 | | |
| Site 6 | 0.279 | 0.271 | 0.319 | -0.076 | 0.539 | 1.179 | |
| | Site 1 | Site 2 | Site 3 | Site 4 | Site 5 | Site 6 | |

Table 6. Cluster analyses of the 10-year family rank data

| | G-series | | I-series | | J-series | |
|---|---|---|---|---|---|---|
| | Discrete | Overlap | Discrete | Overlap | Discrete | Overlap |
| Cluster 1 | Sites 2,4,6 | Sites 4,5,6 | Sites 3,5,7,8 | Sites 3,4,5,7 | Sites 1,2,3 | Sites 1,2,3 |
| Cluster 2 | Sites 3,5,7 | Sites 2,3,6,7 | Sites 1,4 | Sites 1,4 | Sites 4,5,6 | Sites 2,3,5,6 |
| Cluster 3 | | Sites 2,4,5 | | Sites 5,7,8 | | Sites 1,2,4 |

Notes: Discrete clusters produced by Procedure VARCLUS (SAS Institute Inc. 1982). Overlapping clusters produced by Procedure OVERCLUS (Sarle 1983).

located outside site region 4S. The remaining site regions can be treated in a similar fashion, to produce the genetic breeding zones shown on Map 2. Site regions 3E and 3W each contain five genetic breeding zones and site region 4S only four. Given the smaller genotype x environment interaction for the last site region, it is only reasonable that there should be fewer breeding zones.

The Ontario Ministry of Natural Resources, which is responsible for tree improvement in Ontario, is administratively divided into Regions, each containing a number of Districts. Unfortunately, the boundaries of the Regions do not coincide with site region boundaries. Although most of site region 3E is in the Northern Region, the majority of 3W is in the North-Central Region and almost all of 4S is in the North-Western Region. Thus there is some overlap. In addition, of course, the boundaries of the proposed genetic breeding zones for black spruce are not the same as the District boundaries (Map 3) or the forest management agreement boundaries, which are administratively the most convenient. Since it is unlikely to be feasible to have a single district or a single forest management agreement area divided among three or more breeding zones, some compromise must be reached whereby administrative and breeding zone boundaries coincide as closely as possible.

The following, tentative, breeding zones are therefore suggested as a basis for black spruce tree improvement in northern Ontario, until more reliable information is available:

Northern Region:
- Zone 1 - northern Hearst district
- Zone 2 - southern Hearst district
- Zone 3 - Kapuskasing and Cochrane districts
- Zone 4 - Kirkland Lake, Timmins, and Gogama districts
- Zone 5 - Chapleau district

North-Central Region:
- Zone 1 - Geraldton district
- Zone 2 - Terrace Bay and White River districts
- Zone 3 - southern Nipigon, Thunder Bay, and Atikokan districts
- Zone 4 - northern Nipigon district

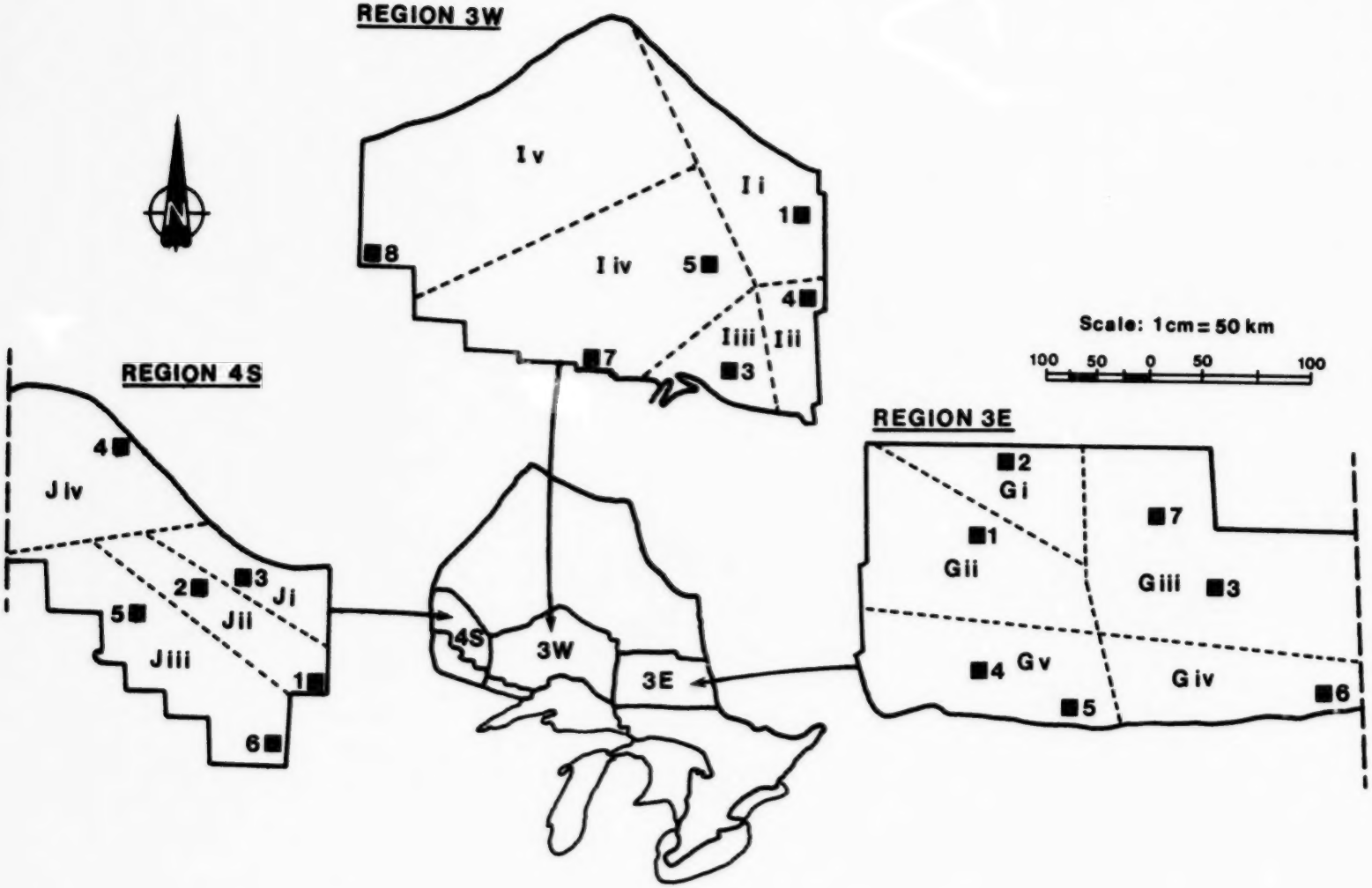
North-Western Region:
- Zone 1 - eastern Ignace and Sioux Lookout districts
- Zone 2 - western Ignace and north-eastern Dryden districts
- Zone 3 - south-western Dryden, Fort Francis, and Kenora districts
- Zone 4 - Red Lake district

4. Means separation.

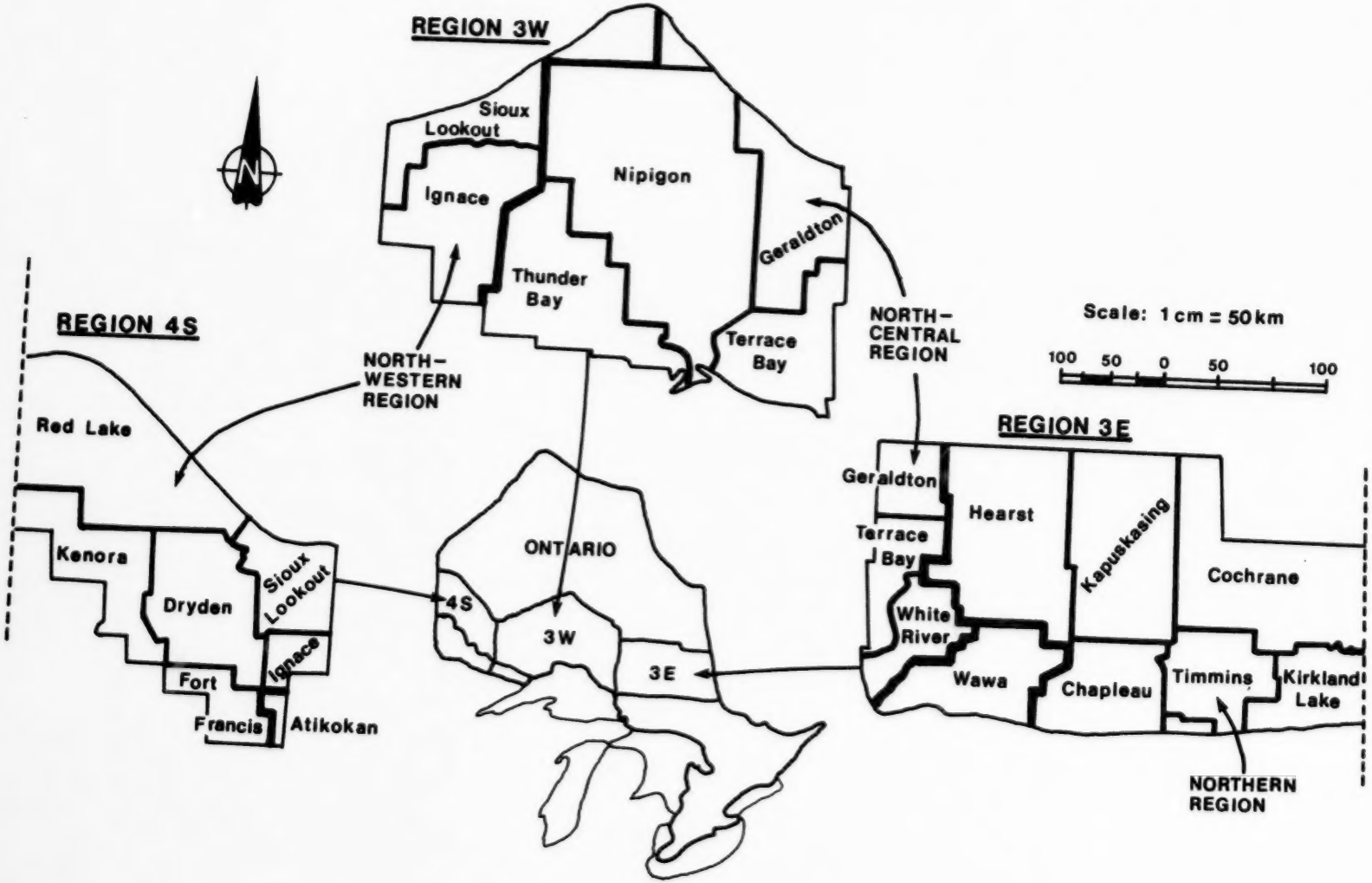
As noted earlier, one of the objectives of these series of progeny tests was to identify superior families for inclusion in breeding programmes (Morgenstern 1978). Although the amount of material required for such programs is very much greater than can be generated by selection in these progeny tests, at least some contribution can be made (Morgenstern 1978). For each genetic breeding zone, the average performance of all families at those sites for which results should be included was calculated. The tallest 20

Map 2. Genetic breeding zone for the three site regions

■ Location of test sites



Map 3. Regions and districts of the Ontario Ministry of Natural Resources



families in each genetic breeding zone are listed in Table 7, together with the stand rankings. Families which formed homogeneous groups by the Scott-Knott means separation method are distinguished by solid lines.

In the G-series, stand 73 is ranked among the top three stands for all five breeding zones. Families in stand 73 originated from a seedling seed orchard established by Spruce Falls Power and Paper Company in 1951 at their Moonbeam Nursery, Kapuskasing, using mass-selected seedlings. Since these trees had already undergone partial selection in the form of mass selection in the nursery, it is not surprising that many of the families rank very highly in several of the breeding zones. Among those stands which were represented in the range-wide provenance tests, there are some anomalous results. In the Chapleau provenance test, the only provenance test in Region 3E, stand 6 ranked second out of 56 provenances at 15 years of age. However, families from this stand performed very poorly in all the proposed breeding zones, being among the bottom two in each case.

Again, in the I-series there is some degree of disagreement between the results of the provenance and the progeny tests. Stand 32 was the worst of the seven stands represented in the provenance test at Thunder Bay. At the other provenance test in Site Region 3W, it ranked fifth of the seven stands. However, it ranked first or second in all breeding zones except Zone I i. Stand 93, which originated from open-pollinated seed from the Kimberley-Clark clonal orchard at Longlac, was the poorest stand in every zone.

Finally, in the J-series, stand 25, which was the tallest in the Dryden provenance test (6th overall) is only average or poor in the progeny tests. On the other hand, stand 18 (2nd of the seven J-series stands in the provenance test) is also first or second in every breeding zone. There is a striking contrast between breeding zones J iii and J iv. In the former, the tallest four plus the sixth tallest families all come from stand 28 (Atikokan), whilst in the latter none of the tallest 20 families come from this stand. Thus, these two breeding zones should be distinguished at all costs.

## CONCLUSIONS

It is clear, both from the single-location and multi-location estimates, that narrow sense family heritability for height growth in black spruce is several times larger than single-tree heritability. The main implication of this result is that the selection of superior genotypes based on progeny testing is far more efficient than by plus-tree selection. In terms of economic gain, therefore, rapid, low intensity selection should be practiced for black spruce in Ontario.

In comparison with earlier estimates of heritability from nursery tests, the estimates obtained from this 10-year-old material are substantially lower. The expected genetic gains per unit time will therefore be correspondingly reduced. However, based on results from other species (eg. Birot and Christophe 1983), estimates of heritability may be expected to stabilize from about this age onwards.

Table 7. The tallest 20 families for each genetic breeding zone, their heights at age 10 (cm), and the rankings of the stands.
Scott-Knott clusters of families are separated by solid lines
In the family numbers, the first two figures represent the stand number and the last two figures the tree number

G-series

| Rank | Zone G i | | Zone G ii | | Zone G iii | | Zone G iv | | Zone G v | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5102 | 128.42 | 712 | 112.35 | 1503 | 137.36 | 1503 | 137.36 | 1503 | 110.93 |
| 2 | 1503 | 110.93 | 904 | 111.11 | 5102 | 128.42 | 5102 | 128.42 | 7321 | 102.72 |
| 3 | 5103 | 105.40 | 1503 | 110.93 | 1504 | 117.64 | 1504 | 117.64 | 905 | 100.12 |
| 4 | 1504 | 100.04 | 7321 | 110.74 | 807 | 110.19 | 807 | 110.19 | 1504 | 100.04 |
| 5 | 7341 | 99.20 | 5075 | 108.13 | 1502 | 109.07 | 5105 | 108.61 | 712 | 99.05 |
| 6 | 905 | 95.22 | 7341 | 104.92 | 5105 | 108.61 | 5103 | 105.40 | 7326 | 98.78 |
| 7 | 7321 | 94.71 | 707 | 102.67 | 7311 | 108.15 | 7341 | 100.43 | 7313 | 98.40 |
| 8 | 7326 | 94.26 | 7313 | 102.40 | 7341 | 107.53 | 7323 | 97.58 | 7331 | 98.24 |
| 9 | 712 | 93.46 | 7326 | 102.15 | 5103 | 105.40 | 7313 | 97.00 | 7341 | 98.21 |
| 10 | 7311 | 93.33 | 7331 | 101.00 | 905 | 103.16 | 7326 | 96.46 | 7315 | 97.42 |
| 11 | 5105 | 93.30 | 1504 | 100.20 | 7323 | 103.15 | 7311 | 95.98 | 7332 | 95.71 |
| 12 | 601 | 93.05 | 7328 | 99.94 | 601 | 102.94 | 601 | 95.89 | 7328 | 94.98 |
| 13 | 7332 | 92.35 | 905 | 99.57 | 614 | 102.18 | 905 | 95.56 | 7335 | 94.00 |
| 14 | 7313 | 92.24 | 7332 | 98.56 | 7332 | 101.83 | 7345 | 95.42 | 904 | 93.95 |
| 15 | 7323 | 92.13 | 806 | 97.80 | 7324 | 100.04 | 7321 | 94.82 | 1405 | 93.93 |
| 16 | 5101 | 91.90 | 7319 | 97.32 | 7335 | 99.49 | 7332 | 94.58 | 707 | 93.16 |
| 17 | 1502 | 91.14 | 7315 | 97.17 | 1513 | 99.47 | 7324 | 94.11 | 7319 | 92.91 |
| 18 | 807 | 90.74 | 911 | 96.91 | 7327 | 99.12 | 5085 | 93.93 | 911 | 91.94 |
| 19 | 1405 | 90.74 | 1405 | 96.86 | 7340 | 98.89 | 1502 | 92.76 | 7324 | 91.82 |
| 20 | 7331 | 90.70 | 1502 | 96.32 | 7326 | 98.42 | 7331 | 92.13 | 7320 | 91.70 |

Stand rankings

| Rank | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 51 | 91.09 | 9 | 91.84 | 51 | 101.34 | 51 | 98.64 | 73 | 88.85 |
| 2 | 73 | 85.28 | 73 | 91.49 | 15 | 94.10 | 73 | 87.10 | 9 | 87.69 |
| 3 | 50 | 84.05 | 50 | 87.28 | 73 | 90.60 | 9 | 85.06 | 7 | 84.06 |
| 4 | 9 | 83.58 | 7 | 87.28 | 9 | 87.91 | 15 | 83.63 | 50 | 84.05 |
| 5 | 7 | 82.75 | 8 | 82.29 | 7 | 86.90 | 7 | 82.82 | 15 | 81.89 |
| 6 | 8 | 78.80 | 15 | 82.22 | 8 | 84.16 | 8 | 80.21 | 8 | 78.32 |
| 7 | 15 | 78.41 | 51 | 78.28 | 14 | 83.44 | 50 | 77.19 | 51 | 78.18 |
| 8 | 6 | 76.75 | 6 | 77.64 | 50 | 81.06 | 6 | 76.08 | 6 | 77.15 |
| 9 | 14 | 73.33 | 14 | 76.18 | 6 | 80.75 | 14 | 72.93 | 14 | 74.30 |

Stand rankings in range-wide provenance tests (Boyle 1985b)

| | |
|---|---|
| 6 | 23rd |
| 15 | 25th |
| 14 | 44th |
| 9 | 47th |
| 7 | 49th |
| 8 | 62nd |

Table 7 (cont'd)

I-series

| Rank | Zone I i | | Zone I ii | | Zone I iii | | Zone I iv | | Zone I v | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2007 | 117.48 | 1910 | 121.34 | 3203 | 134.17 | 1900 | 116.48 | 1008 | 130.95 |
| 2 | 1814 | 109.73 | 1900 | 116.48 | 1910 | 121.34 | 3208 | 115.96 | 1804 | 123.92 |
| 3 | 3208 | 109.39 | 3208 | 115.96 | 1814 | 118.25 | 1910 | 111.10 | 3208 | 122.54 |
| 4 | 1705 | 107.62 | 1809 | 115.88 | 1711 | 117.32 | 3203 | 110.73 | 1913 | 122.04 |
| 5 | 1809 | 107.22 | 3209 | 115.63 | 1900 | 116.48 | 1814 | 110.36 | 1912 | 122.00 |
| 6 | 1707 | 105.88 | 1609 | 111.16 | 3208 | 115.96 | 1809 | 109.96 | 1900 | 116.48 |
| 7 | 1609 | 105.24 | 1814 | 110.79 | 1809 | 115.88 | 1901 | 109.48 | 1910 | 115.17 |
| 8 | 1813 | 105.07 | 1810 | 110.72 | 3209 | 115.63 | 1711 | 107.74 | 1805 | 114.22 |
| 9 | 1906 | 104.35 | 3203 | 108.96 | 2014 | 113.40 | 1805 | 107.49 | 1001 | 112.35 |
| 10 | 1704 | 103.99 | 1711 | 108.80 | 2012 | 112.71 | 3201 | 106.70 | 1809 | 110.88 |
| 11 | 1811 | 103.36 | 1608 | 106.76 | 3202 | 112.56 | 1715 | 106.57 | 3203 | 110.73 |
| 12 | 1702 | 102.02 | 9323 | 106.55 | 3201 | 112.55 | 3202 | 105.11 | 3207 | 109.64 |
| 13 | 1701 | 100.56 | 1702 | 104.82 | 1901 | 112.27 | 1912 | 104.54 | 1901 | 109.48 |
| 14 | 1916 | 100.27 | 1714 | 104.53 | 1715 | 111.88 | 1001 | 104.16 | 1603 | 108.96 |
| 15 | 1001 | 100.08 | 2007 | 104.05 | 1714 | 111.80 | 1609 | 103.88 | 1608 | 108.73 |
| 16 | 1708 | 99.89 | 1907 | 103.33 | 1805 | 111.54 | 3209 | 103.41 | 1606 | 108.36 |
| 17 | 1907 | 99.85 | 2011 | 102.93 | 1609 | 111.16 | 1603 | 103.11 | 1610 | 108.36 |
| 18 | 1915 | 99.46 | 1805 | 102.89 | 1810 | 110.72 | 3207 | 102.84 | 1711 | 106.71 |
| 19 | 1810 | 99.24 | 3207 | 102.84 | 1702 | 110.30 | 1606 | 102.22 | 3201 | 106.70 |
| 20 | 1912 | 99.14 | 1912 | 101.84 | 1902 | 109.34 | 2014 | 102.20 | 1715 | 106.57 |

Stand rankings

| Rank | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 17 | 93.17 | 32 | 96.62 | 32 | 101.65 | 19 | 97.42 | 32 | 103.59 |
| 2 | 18 | 91.92 | 19 | 96.31 | 19 | 99.74 | 32 | 96.56 | 19 | 99.06 |
| 3 | 19 | 88.44 | 17 | 95.78 | 17 | 99.74 | 17 | 96.16 | 16 | 97.15 |
| 4 | 20 | 85.97 | 18 | 95.09 | 18 | 98.73 | 18 | 95.60 | 18 | 97.15 |
| 5 | 16 | 85.61 | 16 | 92.64 | 20 | 94.25 | 16 | 92.96 | 17 | 93.63 |
| 6 | 32 | 84.65 | 20 | 90.19 | 16 | 94.15 | 20 | 90.30 | 10 | 91.35 |
| 7 | 10 | 82.65 | 10 | 85.06 | 10 | 87.76 | 10 | 87.13 | 20 | 89.28 |
| 8 | 93 | 71.25 | 93 | 75.90 | 93 | 76.30 | 93 | 75.86 | 93 | 78.21 |

Stand rankings in range-wide provenance tests (Boyle 1985b)

| | |
|---|---|
| 18 | 5th |
| 19 | 7th |
| 16 | 17th |
| 20 | 18th |
| 10 | 19th |
| 17 | 20th |
| 32 | 30th |

Table 7 (cont'd)

J-series

| Rank | Zone J i | | Zone J ii | | Zone J iii | | Zone J iv | |
|---|---|---|---|---|---|---|---|---|
| 1 | 2815 | 174.30 | 2815 | 174.30 | 2815 | 174.30 | 1810 | 160.30 |
| 2 | 2514 | 146.30 | 1810 | 160.30 | 2812 | 161.06 | 2517 | 160.04 |
| 3 | 2813 | 144.79 | 2514 | 146.02 | 2811 | 156.88 | 2403 | 155.12 |
| 4 | 2812 | 144.21 | 2813 | 144.79 | 2814 | 148.40 | 3112 | 153.36 |
| 5 | 3110 | 139.35 | 2812 | 144.21 | 2514 | 146.30 | 2215 | 152.75 |
| 6 | 2811 | 138.85 | 3110 | 139.35 | 2813 | 144.79 | 2402 | 147.55 |
| 7 | 1803 | 136.97 | 2811 | 138.85 | 2306 | 142.73 | 1814 | 146.02 |
| 8 | 2510 | 134.86 | 1803 | 136.97 | 3110 | 139.35 | 2514 | 145.74 |
| 9 | 2509 | 134.16 | 2311 | 135.76 | 1804 | 138.73 | 1807 | 145.74 |
| 10 | 2311 | 134.05 | 2510 | 134.86 | 2510 | 136.84 | 2302 | 145.24 |
| 11 | 3111 | 133.00 | 2509 | 132.53 | 2311 | 134.84 | 3114 | 140.98 |
| 12 | 2306 | 130.89 | 3111 | 132.35 | 3111 | 133.00 | 2413 | 139.95 |
| 13 | 2802 | 129.00 | 2211 | 129.74 | 1811 | 132.62 | 2305 | 139.53 |
| 14 | 2512 | 128.68 | 2802 | 129.00 | 2509 | 132.30 | 2207 | 138.78 |
| 15 | 1804 | 127.42 | 2517 | 128.93 | 1803 | 131.71 | 2201 | 138.29 |
| 16 | 1811 | 127.00 | 1804 | 127.42 | 2802 | 131.71 | 2510 | 137.67 |
| 17 | 2814 | 126.71 | 2512 | 126.94 | 3108 | 131.58 | 2211 | 137.51 |
| 18 | 3108 | 126.67 | 2407 | 126.78 | 2810 | 127.80 | 1803 | 136.97 |
| 19 | 2307 | 125.96 | 2814 | 126.71 | 2307 | 125.96 | 2407 | 136.49 |
| 20 | 2809 | 125.68 | 3108 | 126.67 | 1802 | 125.93 | 2214 | 135.71 |

Stand rankings

| Rank | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1 | 28 | 126.26 | 28 | 127.23 | 28 | 131.30 | 18 | 132.45 |
| 2 | 18 | 116.00 | 18 | 123.87 | 18 | 114.76 | 24 | 131.47 |
| 3 | 31 | 113.83 | 24 | 117.39 | 31 | 113.58 | 22 | 131.15 |
| 4 | 23 | 113.77 | 25 | 117.16 | 23 | 112.51 | 25 | 127.13 |
| 5 | 25 | 112.30 | 22 | 116.61 | 25 | 110.30 | 31 | 126.15 |
| 6 | 22 | 111.68 | 31 | 116.46 | 24 | 109.25 | 23 | 125.95 |
| 7 | 24 | 110.83 | 23 | 115.47 | 22 | 109.14 | 28 | 116.25 |

Stand rankings in range-wide provenance tests (Boyle 1985b)

| | |
|---|---|
| 23 | 4th |
| 18 | 5th |
| 25 | 10th |
| 24 | 11th |
| 31 | 24th |
| 28 | 39th |
| 22 | 42nd |

Results from the overlapping cluster analysis suggest that four or five genetic breeding zones can be identified in each site region. Since the boundaries of these zones do not correspond with administrative districts, some compromise in the delineation of practical breeding zones is required. The zones proposed in this report can be used to provide an initial organization for black spruce improvement programs. Although modifications and improvements will be necessary as more information becomes available, the use of the suggested breeding zones will ensure a greater genetic gain than would be achieved without recognizing any zones, or by designing purely arbitrary zones.

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